

*Fontelicella* (PROSOBRANCHIA: HYDROBIIDAE),  
A NEW GENUS OF WEST AMERICAN FRESHWATER SNAILS<sup>1</sup>

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ABSTRACT

*Fontelicella*, g. n., (subfamily Hydrobiinae) includes 3 subgenera: *Fontelicella* s.s. (type *F. californiensis*, sp. n.), with 8 species, Pliocene to Recent, of western U. S. A. and Baja California, México; *Natricola*, subg. n. (type *Pomatiopsis robusta* Walker, 1908), with 3 species living in the Snake River drainage of Idaho and Wyoming, U. S. A.; and *Microamnicola*, subg. n. (type *Amnicola micrococcus* Pilsbry, 1893), with 1 species living in the Amargosa River drainage of southern Nevada and southeastern California, U. S. A. Among adequately described species, the most similar is *Cincinmatia integra* (Say) of eastern U. S. A.; it differs in details of verge, radula, pigmentation, shell, and foot. The described features of *Fontelicella* spp. include general form, locomotion, behavior, pigmentation, external morphology, radula, verge, eggs, and habitat. Arrangement of melanin and calcareous granules in the head region is a particularly useful source of specific characters that has been generally neglected in previous work on the family.

The generally small and characterless shells of the Hydrobiidae have rarely been sought by collectors in western North America. There are even less biological data available for this unpopular group than in many others, so from species to family rank their classification is obscure. Our studies have aimed at a partial survey of the western American species, trying to understand their histories and distribution, and to fit the known fossil record into a biological framework.

Preparation of a detailed, illustrated account of the species will require further work, but our observations so far are comprehensive enough to permit

definition of a new genus. We publish this paper to validate use of the names in other papers in progress.

DIAGNOSIS

Family Hydrobiidae

Subfamily Hydrobiinae

*Fontelicella*<sup>3</sup> Gregg and Taylor, new genus

Diagnosis. Shell 2.5-8 mm long in adults, rimate or imperforate, narrowly elongate to conic or globose, with 3-6 whorls, the aperture 20-40% of total shell length. No sculpture except for

<sup>1</sup>Contribution No. 4, Western American Freshwater Mollusks Program, Institute of Malacology.

<sup>2</sup>Research by Gregg was partially supported by National Science Foundation grant GB-1653.

<sup>3</sup>Latin *fons*, *fontis*, a spring; *helix*, *helicis*, a snail, and the feminine diminutive, *-ella*. Hence, little spring snail. The name refers to a characteristic habitat of the group.

minute growth striae. Embryonic shell helicoid, umbilicate, with about 1 1/2 whorls. Verge bifid, with a narrow, melanin-pigmented penis, and a usually wider, virtually unpigmented, ductless accessory process on the left. Accessory process usually with a terminal glandular lobe, subterminal constriction, and additional glandular areas in the form of ridges, lobules or papules. Radula with formula 15 to 30: 17 to 24: 3 to 6-1-2 to 3: 3 to 7-1-3 to 7

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from the second marginal to the central tooth. Eggs laid singly in smooth, unornamented capsules 0.3-0.5 mm in diameter, either free in the substratum or appressed to a firm surface.

Type. *Fontelicella californiensis* Gregg and Taylor, new species.

Remarks. The names applied most commonly to species here referred to *Fontelicella* have been *Paludestrina longinqua* (Gould) and *P. stearnsiana* Pilsbry. One of these two species might therefore have been selected as type of the genus. *Ammicola longinqua* is based on fossil shells and may well be composite. Although the living *Paludestrina stearnsiana* is a recognizable *Fontelicella*, no topotype material can be collected because the growth of Oakland and other cities has destroyed the original habitats. We consider *F. stearnsiana* a valid species on the basis of near-topotypes, but it is more prudent to fix as type species one whose type locality is likely to be available to future students of the group.

The assignment of species described from fossil shells (*Ammicola longinqua*, *A. micra*, *A. pilsbryana*, and *Hydrobia truckensis*), and of the anatomically unknown *Paludestrina cedrosensis* and *Pomatiopsis intermedia*, to the genus is based on shell characters only. Our evaluation of these shell characters is based on knowledge of the anatomy of practically all described western American Hydrobiidae as well as many undescribed forms.

## DESCRIPTION OF GENUS

Study of numerous species (in several genera) of western American Hydrobiidae has revealed sets of characters that unite the group we establish as *Fontelicella*, and distinguish it from other groups. The more conspicuous characters are listed in the generic diagnosis. Less striking features that are common to the described and undescribed species we have examined are summarized below.

General form, locomotion, behavior.

The elongate or globosely conic shell 2.5-8 mm long in adults is borne free of the substratum, with the apex directed upward and posteriorly to the right, so that the axis of the shell forms an angle of about 30°-45° with the long axis of the foot. In dorsal view when the snails are crawling, the snout, tentacles, and eyes are visible in front of the shell. In different species or in different degrees of extension the broadly rounded posterior end of the foot and the anterior corners of the foot may also be visible. Compared to other Hydrobiidae we have seen the snails crawl relatively rapidly; they move smoothly and do not show the stepwise gait of the Pomatiopsinae.

The tentacles are relatively long and slender, rod-shaped, tapering slightly or imperceptibly to blunt tips, about 2/3-3/4 as long as the shell aperture. Cilia may occur in definite longitudinal rows, or scattered with no obvious arrangement. The tentacles are borne diverging at an angle of 70°-100° (90° common), and usually are in vertical or horizontal movement. They move both above and below a plane parallel with the substratum, and often touch the substratum as if sensing it. We have seen no rhythm in motion of the tentacles in any species examined except *F. hendersoni*, in which the tentacles move up and down alternately.

In crawling the snail keeps its snout appressed to the substratum and moves it from side to side. This lateral movement is inconspicuous when the

snail is crawling rapidly, but when moving slowly and feeding the whole head turns from side to side. In animals with less heavily pigmented snouts the action of the radula inside can be seen as the animals browse.

Both direct observation of living snails, and the worn radular teeth show that the snails rasp food from a hard surface as well as pick up fine particulate matter. Field and laboratory observations, and examination of fecal pellets, suggest that the species of *Fontelicella* crudely select detritus from soft mud or browse microorganisms from the surface of stones, dead wood, and decaying leaves.

When observed under a microscope, specimens of *F. hendersoni* showed a positive tropism to the heat or light of the lamp. No other species studied showed this behavior, and it is probably significant that *F. hendersoni* is the only known *Fontelicella* of a warm spring habitat.

**Pigmentation.** The externally visible parts of the body are gray to deep purple-black, from a variably dense suffusion of fine melanin granules. No other pigment is known in *Fontelicella*, in contrast to *Lithoglyphus*, which has both fine melanin granules and larger, yellow-pigment granules. The other elements of color in *Fontelicella* are internal organs, ingested food, fecal pellets, algal or other coating on the outside of the shell, and abundant calcareous granules scattered through most of the head-foot mass and concentrated behind the eyes.

The pattern of pigmentation is specifically diagnostic in nearly all species of *Fontelicella* we have examined, and there are even more marked differences between the genera of Hydrobiidae. Our work thus yields results similar to those of Muus (1963), who found differences in pattern between 3 Danish species of *Hydrobia*. Although each colony of snails may have considerable variability in the density of melanin from one individual to another, in nearly all species the arrangement of melanin and calcareous

granules in the head region is distinctive. Future work on Hydrobiidae should include critical attention to these features as a source of taxonomic characters.

The externally visible body of species of *Fontelicella* varies in color from gray to deep purple-black, but generally the melanin is not uniformly diffused. The dorsal and lateral aspects of the snout and the operculigerous lobe are most deeply pigmented, and ends and sides of the foot, and ventral aspect of the snout less pigmented. The tentacles may be pigmented with diffuse melanin granules like the head, or paler in contrast, but lack discrete patches or bands. When the tentacles are deeply pigmented and bear a discrete ciliary tract, the ciliated strip is outlined as a less heavily pigmented area.

The eyes are set in swellings on the outer bases of the tentacles, and appear as intense black spots within a clear area. A dense, conspicuous aggregation of white granules adjacent to each eye is characteristic of the genus. These granulose areas often give the appearance of eyebrows when they are narrow regions immediately above and behind the eyes. They also may be larger and more diffuse, extending posteriorly on the dorsum of the head, or they may lie in front of the eyes on the lateral aspect of the tentacles.

The sole of the foot in ventral and lateral views can be seen to be unpigmented. When the upper surfaces of the foot are deeply pigmented the color change is abrupt, at a line running around the edge of the foot just above the sole. The lips are lightly pigmented in contrast to the snout.

Pigmentation of the mantle, organs in the mantle cavity, and upper head-foot varies considerably from species to species. The mantle may be opaque, or so lightly pigmented that the stomach, intestine, and outlines of the ctenidial lamellae are visible. The density of melanin decreases from the foot upward, so that the body stalk and floor of the

mantle cavity are virtually unpigmented. The free portion of the penis is densely suffused with melanin granules and is in contrast to the light, unpigmented accessory process.

Head-foot mass. The sole is about 2-3 times as long as wide when the snail is crawling rapidly, but varies in proportions with rate of travel. It is broadly rounded at the hind end, with parallel sides, and widened by 2 auriculate lobes at the anterior corners. The anterior border of the sole is straight or slightly concave. An anterior pedal groove traverses the anterior edge of the foot; into this groove the anterior mucus glands discharge their secretions.

Scattered through the connective tissue of the head-foot mass, mantle border, and externally visible walls of the pallial cavity are numerous relatively large hyaline granules. These are visible only where there is no dense epithelial suffusion of melanin, and likely are spread through all the head-foot mass, except that they are rare in the tentacles.

The highly contractile snout is about  $\frac{1}{3}$  as wide as the foot, flattened-oval in cross-section, and more convex dorsally. Ordinarily it is appressed to the substratum in front of the foot, but the anterior edge of the foot can be stretched farther forward than the end of the snout. Two fleshy pads at the end of the snout together form a roughly oval area in anterior view, narrower dorsally. They are divided in the median plane by the slit of the mouth, and set off from the more deeply colored snout by a narrow constriction.

Mantle cavity. The mantle cavity has the usual organization of hydrobiid snails. From the roof of the cavity the ctenidium hangs down as a series of triangular lamellae forming a ridge that divides the cavity lengthwise into 2 approximately equal parts. To the left on the mantle lies the osphradium, and to the right close to the junction of the roof and floor of the cavity is the rectum. The pallial oviduct lies between the rectum

and right side of the mantle cavity in the female. The large verge fills much of the cavity in the male.

Circulation in the mantle cavity is simple, with a fairly strong inhalant current on the left side and a perceptibly weaker exhalant current out of the right side. Ciliated epithelium carries particles to be rejected from the floor of the mantle cavity down the right side of the body stalk to the edge of the sole, along which they are carried to the hind end of the foot. This ciliated area has sufficient force to carry a fecal pellet up out of the mantle cavity and to the rear of the foot when a snail is held on its back. The exhalant current is usually inadequate to this task. Ciliated epithelium on the left side also carries particles down the body to the edge of the sole and thence posteriorly.

The ctenidium consists of about 14-30 triangular lamellae hanging down from the mantle into the mantle cavity. It is nearly colorless and extends from just inside the thickened mantle border to the rear end of the mantle cavity.

The fecal pellets are ovoid or spindle-shaped, as in all Hydrobiidae seen, and arranged lengthwise in the rectum. They contrast with the cigar-shaped pellets of Pleuroceridae that are arranged transversely in all but the most distal part of the rectum. Representative measurements of the fecal pellets of *Fontelicella* are .12 x .28 mm (*F. hendersoni*) and .11 x .25 mm (*F. californiensis*). They are composed of vegetable fibres and tiny rock particles, with no evident internal structure. The pellets are voided singly as a rule, but sometimes 2 pass through the anus linked by a strand of mucus and fecal material.

Verge. The verge is attached to the floor of the mantle cavity, to the right of the midline and behind the right tentacle. It is relatively large compared to other organs in the mantle

cavity, and although directed forward does not usually protrude from the cavity. The forward direction of the verge is in contrast to that of some other genera, such as *Lithoglyphus* and *Amnicola*, in which the verge curves to the left from its attachment and extends through the median plane.

The relative size of the accessory process and free portion of the penis vary greatly. In *Fontelicella stearnsi-ana* the accessory process is about 1/4 as long, and slightly narrower than the free penis. In *F. idahoensis* it is twice as long and about 6 times as wide as the base of the free part of the penis. Most species of *Fontelicella* have an accessory process with complicated ornament of small discrete glandular areas that appear as low raised areas, circular or elongate in plan, or as secondary lobes that may reach nearly the size of the rest of the accessory process. The differences in pattern of these glandular areas provide many of the characters used in separation of species.

**Radula.** The odontophore bears about 55 (50 - 67 observed in adults) rows of 7 teeth each. The central tooth is approximately quadrilateral, about 2/3 as high as wide, and widest at the base between the ventrolateral angles. The reflection of the tooth is serrated into a large, central, lanceolate cusp with 3-7 progressively smaller cusps on either side according to the species. The strong basal ridge of the central tooth has a strong basal denticle at its arch on either side. The basal margin is prolonged in the center into a tongue-shaped process extending about as far as the ventrolateral angles. The posterior surface of the tongue-shaped projection is concave, and successive teeth interlock thereby.

The lateral tooth has a broad peduncle, and 6-9 cusps on the reflection. The longest and widest cusp is in the middle; 2-3 are medial and 3-6 lateral according to the species, all becoming smaller

toward the sides. The base of the tooth is bowed ventrally so that there is an area convex ventrally, concave dorsally, by which successive teeth of the lateral series interlock. A ridge runs from this ventrally concave projection to the dorsal margin of the peduncle.

The first marginal tooth is falcate, with a broad peduncle and a blade bearing 17-24 long, slender, sharp-pointed cusps. A ventrally projecting ridge, concave dorsally, extends nearly the whole length of the peduncle and interlocks successive first marginals.

The second marginal tooth is slightly narrower, about as long as the first marginal, but lacks an interlocking ridge. The blade of the tooth is shorter, serrated into 15-30 cusps that are shorter and more slender than those of the first marginal.

**Operculum.** The operculum is as in most Hydrobiinae seen, corneous, paucispiral, with a subcentral nucleus nearer the basocolumellar edge.

## COMPARISON

*Cincinnatia* is the only genus of adequately described Hydrobiidae that shows clear similarities to *Fontelicella*. Features common to *C. integra* (Say) as described by Berry (1943) and to species of *Fontelicella* are a verge with one duct (vas deferens), a relatively large accessory process, and relatively small penis. Differentia are shown in Table 1.

Subgenus *Fontelicella* s.s.,  
new subgenus

**Diagnosis.** Shell small for the genus (2.5-5 mm long, 3-4 whorls in adults). Accessory process usually a little longer than free penis. Habitat small springs, seepages, or small streams, in soft mud among dense aquatic plants, on rocks or sticks. Eggs laid in capsules usually free, or sometimes appressed to substratum, usually difficult to see because of a coating of foreign matter.

**Type.** *Fontelicella* (s. s.) *californiensis*

TABLE 1

Structure	<i>Cincinnatia</i>	<i>Fontelicella</i>
Shell	distinctly umbilicate	imperforate or narrowly perforate
Foot	not auriculate	distinctly auriculate
Snout	lighter colored than head	most heavily pigmented part of body.
Penis	not heavily pigmented with melanin	heavily pigmented with melanin
Accessory process	a) with no terminal lobe set off by subterminal constriction b) about 6 times width of penis base c) lacking glandular tissue	a) nearly always with terminal lobe set off by subterminal constriction b) 2-6 (usually 2-3) times width of penis base c) with several discrete areas of glandular tissue
Central tooth	$\frac{4-1-4}{1-1}$	$\frac{3 \text{ to } 7-1-3 \text{ to } 7}{1-1}$
Lateral tooth	4-1-9	2 or 3-1-3 to 6

Gregg and Taylor, new species.

Distribution. Western United States and northwestern Mexico, in the Great Basin and Pacific drainages. California; Nevada, southeastern Oregon, southeastern Idaho, Utah, Arizona, and Baja California. Known from rocks as old as middle and perhaps early Pliocene. This is the most widespread and speciose group of west American Hydrobiidae.

Referred species.

*Fontelicella* (s. s.) *californiensis* Gregg and Taylor, new species. Southern California and northwestern Baja California.

*Fontelicella* (s. s.) *cedrosensis* (Pilsbry), 1927 (*Paludestrina*). Cedros Island, Baja California.

*Fontelicella* (s. s.) *intermedia* (Tryon), 1865 (*Pomatiopsis*). Owyhee River, Malheur County, Oregon.

*Fontelicella* (s. s.) *longinqua* (Gould), 1855 (*Amnicola*) in part. Subfossil, Colorado Desert, southern California.

*Fontelicella* (s. s.) *micra* (Yen), 1946 (*Amnicola*). Pliocene, Salt Lake Group, Bear Lake County, Idaho.

*Fontelicella* (s. s.) *pilsbryana* (Baily and

Baily), 1952 (*Amnicola*). (= *Amnicola pilsbryi* Baily and Baily, 1951, non Walker, 1906). Bear Lake Valley, southeastern Idaho-northeastern Utah.

*Fontelicella* (s. s.) *stearnsiana* (Pilsbry), 1899 (*Paludestrina*). San Francisco Bay region eastward to Sierra Nevada foothills, California.

*Fontelicella* (s. s.) *truckeensis* (Yen), 1950 (*Hydrobia*). Middle or early Pliocene, Truckee Formation, Churchill County, Nevada.

Subgenus *Natricola*<sup>4</sup>

Gregg and Taylor, new subgenus

Diagnosis. Shell large for the genus (4-8 mm long, 4-6 whorls in adults). Accessory process about twice as long as free penis. Habitat large springs, rivers, or lakes, in mud or sand bottom, on gravel, or on aquatic vegetation. Eggs laid in capsules appressed to substratum.

<sup>4</sup>Latin *natrrix*, *natricis*, a water snake; *-cola*, inhabitant. From the occurrence of most of the species in the Snake River drainage.

Type. *Fontlicella (Natricola) robusta* (Walker), 1908.

Distribution. Snake River drainage of western Wyoming and southern Idaho; Harney Lake Basin, eastern Oregon.

Referred species.

*Fontlicella (Natricola) hendersoni* (Pilsbry), 1933 (*Amnicola*), Harney lake basin, Harney County, Oregon.

*Fontlicella (Natricola) idahoensis* (Pilsbry), 1933 (*Amnicola*), Snake River, southwestern Idaho.

*Fontlicella (Natricola) robusta* (Walker), 1908 (*Pomatiopsis*), Jackson Lake, Teton County, Wyoming.

Subgenus *Microamnicola*<sup>5</sup>

Gregg and Taylor, new subgenus

Diagnosis. Shell small for the genus (1.5-1.7 mm long, 3 1/2 whorls in adults), more nearly ovate. Accessory process beyond fork of verge about half as long as free penis, tapering to a rounded distal end, lacking terminal glandular lobe, subterminal constriction, or other ornamentation. Free penis rod-like, with parallel sides and rounded distal end, heavily pigmented and visible through shell and mantle. Habitat springs, on rocks and aquatic vegetation. Eggs laid in free capsules, less heavily coated with adherent particles than in *Fontlicella s. s.*

Type. *Fontlicella (Microamnicola) micrococcus* (Pilsbry, in Stearns, 1893) (*Amnicola*).

Distribution. Amargosa River drainage, in southern Nye County, Nevada; eastern Inyo County, and northern San Bernardino County, California.

Referred species. Only the type species is known in this subgenus.

*Fontlicella (s. s.) californiensis*<sup>6</sup>

Gregg and Taylor, n. sp.

Diagnosis. Shell about 3-4 mm long

in adults, elongate-ovate, with 4 whorls. Free part of penis moderately pigmented, with a dorsal ridge extending nearly to the tip. Accessory process about as long as free part of penis, and about 3 times as wide at the fork, with a terminal lobe, subterminal constriction, and variable ornamentation, usually including a dorsal lobule, 1-5 dorsal longitudinal ridges, and a ventral transverse ridge. Main body of verge with a dorsal transverse ridge that may unite with the dorsal ridge on the accessory process or penis.

Type. University of Michigan Museum of Zoology catalog number 220000. Campo Creek, San Diego County, California, 0.6 mi. east of Mountain Empire Dam, W 1/2 SW 1/4 sec. 19, T. 18 S., R. 5 E<sup>6</sup>. W. O. Gregg, W. B. Miller, 25-III-1962.

Distribution. Southern California and adjacent Baja California. From the southern Sierra Nevada (on the western slope only) through the western Transverse Ranges and coastal plains to the Laguna Mountains. This species is characteristic of perennial springs and small streams in the mountains. It occurs in both the Pacific Ocean and interior drainages.

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<sup>5</sup>From the Greek word for small, and *Amnicola*.

<sup>6</sup>Named for the Californias, to which it is restricted.

<sup>7</sup>Land in the United States is commonly divided into "townships", each 6 miles square, that are numbered according to tier (T.) and range (R.) from standard base lines and meridians. A township is divided into 36 "sections", each section (sec.) 1 mile square.

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## RESUMEN

*Fontelicella* (PROSOBRANQUIA, HYDROBIIDAE)  
UN NUEVO GENERO DE CARACOL FLUVIAL DEL OESTE AMERICANO

*Fontelicella* g. n. (subfam. Hydrobiinae) incluye 3 subgeneros: *Fontelicella* s.s. (tipo *F. californiensis* sp. n.) con ocho especies del Plioceno al Reciente en el oeste de Estados Unidos y Mexico (Baja California); *Natricola* subg. n. (tipo *Pomatiopsis robusta* Walker, 1908) con tres especies en el sistema del Río Snake de Idaho y Wyoming; *Microamnicola* subg. n. (tipo *Amnicola micrococcus* Pilsbry, 1893) con su única especie viviente en el sistema del Río amargosa del sur de Nevada y sureste de California. Entre especies adecuadamente descritas la más similar es *Cincinnatia integra* (Say) del oriente de Estados Unidos: difiere en detalles de la verga, rádula y pigmentación, concha y pié. Los aspectos descriptos de *Fontelicella* incluyen forma general, locomoción, comportamiento, pigmentación, morfología externa, radula, verga, huevos y habitat. El agrupamiento de gránulos de melanina y calcio en la región cefálica es de particular utilidad como caracter específico, y no había sido tomado en cuenta en previos trabajos sobre esta familia.